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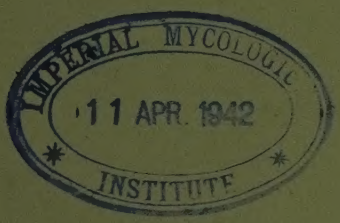

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THE BOTANICAL REVIEW

VOL. I NOVEMBER, 1935 NO. 11

SOME VIEWS ON THE MORPHOLOGY AND PHYLOGENY OF THE LEAFY VASCULAR SPOROPHYTE (CONTINUED)

ISABEL M. P. BROWNE
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THE MEGAPHYLLUS TYPES AS EXEMPLIFIED BY THE FERNS

We have already briefly considered (11*a*) the leafless predecessors of leafy vascular plants, the early microphyllous forms and the forerunners of the megaphyllous types. We must now deal with the typically megaphyllous phylum, the Filicales, *sensu latu*. So far as our present knowledge extends, the Coenopteridaceae are, phylogenetically speaking, the most important group of primitive Filicales. Professor Bower's latest book contains a diagram in which the multitudinous groups of recent ferns, eusporangiate as well as leptosporangiate, are shown as diverging from the Coenopteridaceae (9, *463*). This diagram is not meant to convey the idea, however, that existing families of ferns are descended from any coenopterids known to us, for the author says that the Coenopteridaceae "may be accepted as synthetic types, representing more than any others such approximate sources as those from which the class of the Filicales may have originated" (9, *459*). Scott's position was essentially similar, for he pointed out that while the Coenopteridaceae (his Botryopteridaceae) were too specialized to be the ancestors of modern ferns, the analogies that they present with so many fern families suggest that both groups represent offshoots from the same main line of descent (46, *364*). And later he recognized the probability of "a real if somewhat remote affinity" between the Coenopteridaceae and Ophioglossaceae (47, *413*).

Before considering the Zygopterideae and Botryopterideae, which with the less well known family of the Anachoropterideae constitute the order of the Coenopteridaceae, something must be

said of the scale-like structures known as *aphlebiae*; they are found chiefly in the Zygopterideae but also in some other Palaeozoic ferns. The aphlebiae, originally described as scale-leaves, were interpreted by Dr. Paul Bertrand as equivalent to secondary rachises, the emission of traces to which took place precociously before the leaf-trace had entered the petiole or secondary rachis (4). By far the most satisfactory analysis of the morphology of the aphlebiae yet given is by Dr. Hirmer (21, *573, 690*). He distinguishes between true aphlebiae and aphlebioid structures. The latter may, phylogenetically speaking, represent modified pinnae, or structures of a stipular nature, or, perhaps even in some cases, complete specialized fronds, such as those found in the recent *Trichomanes aphlebioides* Christ. (51), It seems to be largely the failure to draw this distinction which has made certain writers despair of establishing the homology of the aphlebiae (22, *103*). Thus, the so-called aphlebiae of *Diplolabis Römeri* Solms and *Metaclepsydropsis duplex* Will., found at the base of the insertion of the primary [not, as Dr. Holden suggests, at the base of the tertiary (22, *104*)] pinnae have been shown by Dr. Gordon to be specialized pinnae (15, *716*). Curiously enough, Dr. Hirmer alludes to these two species as possessing true aphlebiae (21, *690*). And the so-called aphlebiae of *Austroclepsis* (*Clepsydropsis*) *australis* Osborne are, as Dr. Sahni pointed out in describing this fossil, fairly certainly the homologues of the primary pinnae borne farther up on the petiole (41, *15*). While such aphlebioid structures may be large or small, the true aphlebiae, though they may be branched and possess a branching vascular strand, remain relatively small and represent, phylogenetically speaking, former microphyllous emergences, comparable to those of some Psilophytales, *e.g., Asteroxylon* and *Psilophyton.* Such emergences are held to have originated when the plant body was still thalloid and this would explain why in some species, *e.g., Ankyropteris corrugata* Will., *A. scandens* Stenzel, *A. Brongniarti* Ren.[1] and *Botrychioxylon paradoxum* Scott, they occurred both on the axis and on the

[1] This species is not mentioned in Dr. Holden's summary of the species of *Ankyropteris* possessing aphlebiae, but these were described by Renault as scale leaves and are shown in his figure (38). These figures also show that the petioles were not, as has been stated, whorled (21, *527*), but were given off singly. Where their insertion is not disturbed by the presence of a petiole, it is the aphlebiae that might be described as being whorled or in a close spiral.

leaf. Dr. Hirmer also holds that the relegation of the (true) aphlebiae to special positions on the frond is a derivative condition, occurring in conjunction with a sharper definition of spatial relations. Dr. Scott, in a review of Dr. Hirmer's book, spoke favorably of the latter's account of the aphlebiae and aphlebioid structures (48, *344*), and in his latest book Professor Bower expresses fundamentally similar views (9, 628). Scott had previously accepted the view that the aphlebiae were equivalent to secondary rachises and that they had in certain cases "spread" to the stem (45, *60*).

In the case of the Zygopterideae the most controversial issue is whether the Dineuroideae, where the primary rachis bore four rows of pinnae, or the Clepsydroideae, where it bore but two such rows, was the more primitive. The decision on this point is much influenced by the view taken of *Stauropteris*. Lignier regarded this genus as much more primitive than the other coenopterids which he believed to have arisen from it or from forms allied to it. He even believed it possible that the branch-systems known as *Stauropteris* were not borne on a specialized stem (37). Dr. Hirmer also regards *Stauropteris* as very primitive and derives the other Zygopterideae from some such type, holding that the rachises of the second and, when present, of higher orders, came in the remaining Dineuroideae, presumably in correlation with the exigencies of available space, to be inserted laterally on the parent rachis and to share its plane of symmetry. He considers that in the Clepsydroideae the process was carried a step further and that the primary pinnae underwent the same change in orientation (21, *688*).

Dr. Zimmermann emphasizes very strongly the morphological primitiveness of *Stauropteris* when he says (52, *188*): "In other words, the whole structure still represents, as in the Rhyniaceae and without marked division of labour, the shoot-axis, 'leaves' and 'pinnae' . . . ." Its branch system is held to show an advance on the *Rhynia*-type by being built on a rigidly alternating system of monopodial and dichotomous branching, the pairs of pinnae consisting, properly speaking ("eigentlich"), of a completely reduced lateral branch which dichotomizes at once on leaving the parent axis (52, *189*). This dichotomy does not seem, in Dr. Zimmermann's view, to represent a doubling in phylogeny, such as that

hypothecated by Drs. Bertrand and Sahni, but merely a primitive character retained and taking place precociously in the ontogeny of the frond. Dr. Zimmermann's view of the origin of the flattened and more or less typical frond from some such type as *Stauropteris* is, in essentials, similar to Dr. Hirmer's. Nevertheless, he holds that the petiolar bundle was primitively bipolar, differing only slightly from the *Clepsydropsis*-type in form and in the absence of the small islands of parenchyma abutting on the protoxylems. From such a prototype he derives three or more (52, *195*) main series of zygopterid bundles. Of these, the stauropterid line arises by the antero-posterior division of the two lateral protoxylems and the lobing of the outline of the metaxylem to form the characteristic four-armed *Stauropteris* bundle, giving off vascular strands to four series of branches. In two other main lines the next step is held to have been the median constriction of the bundle and the appearance of two small islands of parenchyma abutting on the protoxylems. Such islands have also been observed once in *Stauropteris* (6). A bundle of the kind found in *Clepsydropsis antiqua* Unger thus results. Doubt has recently once more been thrown on the zygopterid affinity of this species (44), but the argument need not be affected thereby, as a clepsydroid bundle occurs as an early phase of leaf-trace development in several undoubted zygopterids. From this type Dr. Zimmermann postulates the evolution of a series culminating in the biseriate ankyropterids and of another series leading through the quadriseriate *Metaclepsydropsis* to the etapterids. Thus, for him, the similarities between *Stauropteris* and the petiole of *Diplolabis* are due to homoplasy. Dr. Bertrand, whose views on the evolution of the Zygopterideae are very different, also takes this view (5, *225*). Professor Bower apparently shares in this opinion also since, while fully recognizing the doubt that subsists as to the morphology of *Stauropteris,* he speaks of it as the most archaic type among Palaeozoic ferns and as one giving a valid base for comparison with the Psilophytales (8, *269;* 9, *459*) ; he looks upon *Diplolabis* and the other quadriseriate zygopterids as derived from biseriate types by dichotomy of the primary pinnae (*7, 27*). He regards the bipolar bundle as primitive for the family (*7, 27;* 9, *345*). Dr. Leclercq, though she speaks of the suppression of the second or accessory plane of symmetry of the petiolar bundle of certain Zygopterideae leading

to the reduction of the rows of primary pinnae to two, yet seems to accept (in agreement, she says, with French and English authors), the *Clepsydropsis*-type of bundle as primitive for the petioles of the family. She rejects *Clepsydropsis* itself as the direct stock from which *Metaclepsydropsis* might have been evolved on account of its being a biseriate type. But she thinks it not improbable that a form with a clepsydroid foliar bundle, giving off pinna-traces to four rows of appendages, may one day be found to connect *Metaclepsydropsis* and its derivatives with the hypothetical ancestral bipolar bundle (35, *B53, B58*). Dr. Zimmermann argues that a plant such as *Stauropteris* may be primitive in certain characters, *e.g.,* in external morphology and sporangial structure, yet divergently differentiated in other characters such as the disposition of the vascular elements. This is undoubtedly true and the fact that its sporangia seem to be primitive does not imply that the vegetative parts of *Stauropteris* are necessarily also primitive. But the form of the meristele and more especially the development of the lobes or arms of xylem, not only in *Stauropteris* but also in the petiolar bundles of *Diplolabis* and *Etapteris,* seem clearly to be correlated with the emission of four series of traces. So that *if* the flattened bipolar bundle was primitive for the Zygopterideae, then it would seem natural to regard the quadriseriate types as derived from the biseriate ones by a dichotomy, in the phylogeny, of the primary pinnae, and to look upon *Stauropteris* as a specialized zygopterid. This was the view taken by Kidston and Gwynne-Vaughan (25, *469*), by Drs. Bertrand and Sahni (4, 5, 39) and provisionally by Scott (46, *337, 415*). Drs. Gordon and Holden also incline to the view that the primitive zygopteridean petiolar bundle was an oval bipolar one and the latter author further thinks the biseriate forms with permanently closed filaments less specialized than the quadriseriate forms with their more modified secondary and tertiary traces and more strictly localized protoxylem (15, *731;* 16, *187;* 22, *107*).

A new complexion has been put upon the problem of the relation of the quadriseriate to the biseriate zygopterids by Dr. Holden's researches on *Ankyropteris corrugata* Will. This species seems to be primitive in that in it the aphlebiae occur indiscriminately on leaf and axis, and in that it has no axillary branch, the stem branching by equal dichotomy. Dr. Holden has shown that it had

no flattened lamina or pinnae and that the occasional branching of the petiole was always dichotomous and, in the cases observed, at right angles to the bar of the petiolar bundle (*22, 97*). While this form of branching is almost certainly highly primitive, its occurrence in a genus included among the biseriate Zygopterideae, far from suggesting that the biseriate forms are primitive, shows, on the contrary, that the most primitive ankyropterid petioles had not yet evolved the biseriate type of branching characteristic of the Clepsydroideae. We may presumably accept Dr. Holden's suggestion that the dichotomous branching of the petiole was probably found also in the ancestral type of the Zygopterideae, and that when this kind of branching was lost, two series of forms, biseriate and quadriseriate, arose. If this was so, the two pairs of rows of pinnae of the Dineuroideae might naturally be regarded as due to a partial retention of the ancestral dichotomy. But, even if we accept this view, that does not settle the question of whether the petiolar bundle was originally more or less radial or a flattened bipolar one. A final consideration of this point is best postponed until after a short discussion of the allied family of the Botryopterideae, especially of *Botryopteris*.

Botryopteris is a genus of relatively small protostelic forms. A certain similarity between the emission of the leaf-trace and the branching of the stem (*2, 545; 7, 16; 9, 566*) has been held to suggest that the family shows the primitive origin of leaf and axis as shanks of an unequal dichotomy. The similarity is most marked in *B. cylindrica* Will. in which the stem branches dichotomously. This species shows some anatomical variation. In the larger mesarch type of cauline stele, regarded by Dr. Bancroft as more primitive than the monarch one with a central protoxylem, the dichotomy is usually unequal (*2, 561*), and it is this type of cauline branching that the giving off of a petiole most resembles (cf. Scott's fig. 156: 46, *346*). But, whereas the protoxylem of the branch is from the first deeply immersed, the leaf-trace is endarch at its origin, though occasionally a few centripetal tracheides, which soon disappear, are present a little higher up. The large size of the petiole and its bundle, compared to the stem and its stele in *B. antiqua* Kidst., in *B. hirsuta* Will. and in *B. ramosa* Will., might be held to suggest that these forms were still near to those in which stem and leaf were not yet fully differentiated, the more

so that *B. antiqua* is geologically considerably the oldest species. Though still relatively large in *B. cylindrica* and *B. mucilaginosa* Kraentzel (*27*), the petiole and its bundle in these two are smaller compared to the stem and its stele. *B. antiqua* comes from the very base of the Carboniferous; the other species, with the exception of the Lower Permian *B. forensis* Ren., are from the Coal Measures. But caution is necessary. In *B. antiqua* and *B. hirsuta* the petiole is usually larger than the stem and in the former species the leaf-trace and petiolar bundle are from half as large again to twice as large as the cauline stele (*23, 3*). Even in monarch petioles the bundle is often as large or larger than the axial stele. If branch and leaf were originally part of an undifferentiated dichotomizing thallus, one can hardly suppose that it was the larger shank that became appendicular with reference to the smaller! That reduction in size of the stele has occurred in *Botryopteris* is supported by the small size of the axial stele in *B. antiqua* and by the fact that in *B. cylindrica* the smaller monarch and endarch type of stele seems to have arisen from the larger mesarch type (*2, 553*). *B. antiqua* was heterophyllous. Some petioles were monarch and were associated with aphlebioid structures, the trace for which was given off quite close to that of the leaf but diverged from it at once to enter the aphlebioid leaflet which was borne on the other side of the stem. Other leaf traces were diarch and in association with these no aphlebioid structures have been observed. No case is known of two diarch traces being given off in succession. The statement that the two kinds of petioles alternate on the stem (*21, 537*) goes further than the facts warrant. In connection with her text-figure (cf. *3, 1051*), Dr. Benson speaks of the "very common monarch petiole bundle" as though diarch forms were less common. Dr. Benson suggests that diarch petioles might have arisen from monarch by an "arrest of branching at a primary phase," and that this view could be extended to the triarch petioles (those of *B. ramosa* and *B. hirsuta*) which might "well bear the same relation to the diarch forms as the latter bear to the monarch forms" (*3, 1051*). This view is held to be supported by the similarity between a branching diarch petiole of *B. antiqua,* in which the protoxylem of the pinna-trace is individualized some distance below its departure, and a non-branching triarch petiole of *B. ramosa.* It is certainly possible to construct a series starting with the monarch petioles of

B. antiqua. From this species the development passes through the diarch forms found in it and in *B. cylindrica,* wherein monarch petioles with the protoxylem spread along the adaxial side sometimes occur (2), to the typically triarch petioles of *B. ramosa* and *B. hirsuta.* In these the protoxylems are at the end of three short adaxial projections. Ultimately, through the newly described *B. mucilaginosa* Kraentzel, with three slightly more projecting protoxylems, the series runs to *B. forensis* Ren. in which the three projections have become long arms and the protoxylems are more numerous.[2] The generally held view that *B. forensis,* the geologically youngest species, is a derivative type, may be accepted as regards the length of the arms (5, *230;* 46, *350;* 7, *13;* 9, *343;* 27, *M68*). But it should be noted that the petiole of *B. forensis* is fundamentally diarch and not triarch. There are only two main groups of protoxylem (Bertrand's "pôles fondamentaux"), one on each side of the middle arm of metaxylem. The numerous other groups of protoxylem are cut off from these and, detaching themselves from the metaxylem for a short space, they work their way backwards along the lateral arms and pass out as parts of pinna-traces (4, *231*). They merely represent an extreme example of the early individualization of the protoxylem of a pinna-trace, such as that recorded by Dr. Benson in the branching diarch petioles of *B. antiqua* (3, *1048*). It is, however, an open question how the series formed by the remaining petioles should be read. Dr. Benson's view that the monarch type is primitive has been widely accepted (5, *233;* 2, *558;* 7, *13, 36;* 9, *343;* 27). Dr. Hirmer, however, regards the monarch petioles as derived from diarch ones by one half of the bundle assuming a median position and the other becoming laterally displaced and entering the aphlebioid pinnule. He erroneously attributes a similar view to Dr. Benson (21, *538*). The view that the monarch types are reduced, gains some support from the considerations already advanced, tending to show that the stele has undergone reduction in *B. antiqua;* while the heterophylly of this species can hardly be regarded as a primitive character.

As long ago as 1910 Kidston and Gwynne-Vaughan suggested a common origin for Osmundaceae and Zygopterideae and held

[2] Cf. 27; 5, *31,* Fig. 26, a figure reproduced by Dr. Hirmer as of *B. tridentata* Felix (=*B. hirsuta* Will.) 21, *535.* Fig. 651. On the other hand, Dr. Zimmermann's (original) figure labelled *B. forensis* Ren. (52, *195,* Fig. 129) is apparently not a petiole of this species. It may belong to *B. hirsuta* Will. or more probably to *B. ramosa* Will. (34, Pl. 42).

that the petiolar structure of the former was the more primitive. They pointed out that in the Permian *Thamnopteris,* some of the traces possessed, in the neighborhood of the stele, "two immersed protoxylems situated at points more or less apart from the centre of the strand" (25, *469*). These traces show an approach in structure to *Clepsydropsis,* the petiolar bundle of which they regarded as primitive for the Zygopterideae. *Thamnopteris* is one of the oldest of the Osmundaceae and now generally accepted as showing, with *Zalesskya,* the most primitive and definitely osmundaceous known stelar structure (46, *278;* 21, *596;* 52, *211;* 7, *136*). In *Thamnopteris Schlechtendali* Eichw., the leaf-trace is given off as an oval strand with a single central protoxylem. As this strand passes through the cortex, some of the centripetal tracheides next to the protoxylem cease to be formed, so that a small parenchymatous island arises. This island enlarges tangentially and adaxially and the protoxylems multiply by division until the xylem has become C-shaped with protoxylem groups along its adaxial concavity. Eventually, the trace assumes the same contour as the xylem. Gwynne-Vaughan and Kidston suggested that the changes undergone by this trace in passing through the cortex represent the phylogenetic steps that have led to the development of the monodesmic C-shaped strand, generally recognized as primitive for the Osmundaceae and for the great majority of the Leptosporangiatae (18). They, therefore, regarded a simple monarch petiolar bundle as primitive for the Zygopterideae and the Osmundaceae. Dr. Bertrand accepted this view and extended it to the Botryopterideae (5, *233, 280*). For him, Botryopterideae and Zygopterideae were much more closely allied to one another than to the Osmundaceae. He regarded the Botryopterideae as less specialized than the Zygopterideae and more easily comparable to the Osmundaceae. He looked upon the monarch petiolar bundle of *Botryopteris antiqua* as primitive and compared it with that of *Thamnopteris.* The analogy is not so close as he suggested, however, since there seems to be no authority for his statement that the xylem of the trace of *B. antiqua* passes through a phase in which it has an excessively reduced parenchymatous island. He suggested that the primitive petiolar bundle for the three families was either a ring of endarch xylem, enclosing a central island of parenchyma, or a solid strand of xylem with a single central protoxylem. The former hypothesis

has received little or no support but the latter has been accepted in essentials by Professor Bower, among others (*9, 577*).

To summarize the position: There is a considerable measure of agreement among those whose opinion carries weight that the primitive form of leaf-trace for the ferns generally was a single monarch strand; and there is a larger consensus of opinon in favor of the relative primitiveness in the Zygopterideae of the oval bipolar petiolar bundle as compared with the tetrarch one.

Against these views the following considerations are tentatively advanced.

Whether in the earliest vascular plants the xylem was endarch, mesarch or exarch, it is clear that endarchy, mesarchy and exarchy were all established before the cladode megaphyll was differentiated. The exarch *Gosslingia* is as old or older than the endarch *Rhynia major*. Where a protostele has attained a certain size, it is clear that a single group of protoxylem—and a truly endarch protostele can have but one such group—will hardly prove sufficient to establish an early connection of the conducting xylem with the developing parts, especially with the large leaves of the Pteropsida which, as Dr. Zimmermann remarks (*52, 78*), overtake and envelop the axis in their development. And in point of fact, the larger protosteles, when devoid of secondary growth, tend to be mesarch or exarch. Moreover, Professor Bower, in his exhaustive account of the morphology of the ferns, has pointed out again and again the presence of parallel developments both in widely separated and in allied form. He says (*8, 283*): "Further, the progressions in respect of the several criteria are not restricted to any single phylum (of ferns); they are exhibited with a high degree of uniformity in a plurality of phyla, which palaeontology shows to have been broadly distinct from one another in descent from very early periods." Knowing the large size attained by some of the Psilophytales without developing leaves, we are certainly justified in assuming that the megaphyll was differentiated several times independently during the evolution of the ferns, in the wide sense, and in some cases in forms with relatively large exarch or nearly exarch steles. If the megaphyll was originally a but slightly smaller branch of an unequal dichotomy, it is inherently probable that in its early phylogenetic development it would in these cases have carried off several strands of protoxylem. If the stele of the thalloid axis, previous to its

differentiation into stem and leaf, possessed a number, say 10–12, strands of protoxylem in a more or less peripheral position, the weaker branches of the dichotomy might well carry off four of these—or carrying off fewer, might tend by division to restore this number. There is no reason why some of the Zygopterideae, without being in all points primitive, should not have retained in their megaphylls certain characters that belonged to an originally radially constructed branch-system, for instance, the four series of primary pinnae and the approaches to radial symmetry in the foliar bundle of the Dineuroideae. If the biseriate types were primitive, the presence of four arms of xylem and of four main strands of protoxylem in the genus *Ankyropteris* would be hard to explain; but if these characters were a relic of former radial construction their presence in *Ankyropteris* would be more easily explicable. The Zygopterideae are, on the whole, older than the Botryopterideae and much older than the Osmundaceae which have been found below the Permian. Among the Zygopterideae, the Dineuroideae are, as Dr. Hirmer points out, older than the Clepsydroideae, since the structure of the leaf-trace (the free petiole is unknown) in *Asteropteris,* the oldest known zygopterid, makes it almost certain that the leaf branched in the dineuroid manner (21, *506*). It is difficult to accept Professor Bower's description of the trace of *Asteropteris* as a "slight modification" (*7, 27*) of that found in *Clepsydropsis antiqua.* The genera *Stauropteris, Diplolabis, Dineuron* and *Metaclepsydropsis* all have representatives at the very base of the Carboniferous, while even the later genus, *Etapteris,* has one Lower Carboniferous species (*E. Tubicaulis* Goepp.). The only *undoubted* biseriate zygopterid recorded from the Lower Carboniferous seems to be *Austroclepsis* (*Clepsydropsis*) *australis* Osborne (50, *198*) for of *Zygopteris* (Hirmer's *Protoclepsydropsis*) *Kidstoni* P. Bertrand too little is known to include it in either series, and doubts have again arisen as to the zygopteridean affinity of *Clepsydropsis antiqua.* It is not contended that any zygopteridean bundle known to us is wholly primitive. Indeed, the frequently complicated form of the zygopteridean petiolar bundle suggests considerable specialization. It has been shown by comparison on a wide basis of a number of recent ferns, that the task of carrying forward a sufficient supply of water to the distal pinnae falls in many recent ferns on the incurved adaxial elaborations of the petiolar bundle, while in others

the abaxial parts of the bundle undergo amplification (13). It may well be that the prolongation of the abaxial and adaxial arms of the petiolar bundle beyond the points of departure of the pinna-traces and their curvature in certain Zygopterideae (*e.g., Ankyropteris bibractensis* Ren., *A. westphaliensis* P. Bertrand and *Etapteris Scotti* P. Bertrand) are specializations of this nature. Where differentiation of a thalloid axis into stem and leaf took place in forms with a truly endarch protostele and therefore probably in forms with a small stele, a monarch leaf-trace may well have been primitive. Reasons have, however, been given for thinking that in the Botryopterideae endarchy is a derivative character, associated in reduction with the size of the stele. Moreover, in *Botryopteris Fraiponti* Leclercq, which was not considered with the other species of *Botryopteris,* as it is very incompletely known and may have to be made the type of a new genus, the exarch protostele of the very slender stem (or perhaps of a small branch) appears to have 7–10 projecting groups of peripheral protoxylem. The departure of its trace takes place by the giving off of a chunk of metaxylem, including three of the peripheral groups of protoxylem (33). Thus, the xylem of the leaf-trace, at any rate at its origin, is, like that of the stem, wholly exarch and the similarity of the departure of a trace to an unequal dichotomy of the stem would presumably be closer than in *B. antiqua,* although the leaf-trace is only about a quarter of the size of the cauline stele. It is, however, not known if the stem branched dichotomously. If rightly interpreted, this species would seem to be a very primitive member of the Botryopterideae and would strengthen the case for an affinity between *Botryopteris* and *Grammatopteris.* Dr. Sahni has recently come to the conclusion that the affinity between these two genera, characterized by Scott as close (46, *350*), is very remote and that *Grammatopteris* is so closely allied to the Zygopterideae and Osmundaceae that it might be included in either family (43). The arguments against the affinity between *Botryopteris* and *Grammatopteris* are said to rest upon endarchy of the former, the absence of resemblance between the leaf-traces, the habit and phyllotaxy. The habit is hardly of much importance and, as already pointed out, the evidence is against the primitiveness of endarchy in the stem of *Botryopteris.* While the leaf-trace of *Grammatopteris* is admittedly very different from that of a typical *Botryopteris,* its exarchy

may be compared to that of *B. Fraiponti,* a species which, even if it be excluded from the genus *Botryopteris,* appears to be a primitive member of the family. The points of affinity with the Zygopterideae, not shared also with the Osmundaceae, are said to be the differentiated protostele with a stellate core and the bipolar, tangentially elongated foliar bundle, symmetrical in both radial and tangential planes (43, *874*). It is, however, admitted that the protoxylems are sometimes and may, perhaps normally, be adaxial; and in the petiole the smaller tracheides frequently lie more towards the adaxial face of the bundle (43, *869*). The differentiated protostele is found also in the earlier Osmundaceae (21, *596*), while the stellate core seems to have been found only once, near the base of the stem of one specimen and is not very clear there (Cf. 43, Pl. XXXV, Figs. 9 & 10). The affinity of *Grammatopteris* to the Osmundaceae seems clear and it is possible that it should be regarded as the most primitive known member of that group. But there is also an affinity between it and the genus *Botryopteris* and apparently a much closer one than that between *Grammatopteris* and the Zygopterideae though, as the latter family and the Botryopterideae seem to be allied, there appears to be a certain, though a less close relationship between the Zygopterideae and Osmundaceae. The probability seems to be that the three families had a common vascular ancestor which was either a very primitive fern or had progressed a considerable distance along the fern-line. The Zygopterideae constitute the oldest family and seem to have diverged along their own lines, but to have retained in their fronds certain reminiscences of radial organization. The next oldest branch to have differentiated seems to have been that of the Botryopterideae. In them the primary pinnae or the primary branches of the rachis were disposed in two rows and the frond seems to have been dorsiventral, like those of ordinary ferns except, perhaps, in *Tubicaulis solenites* Cotta (Cf. 21, *539* and Figs. 657 and 658). But in the most primitive forms of this line the petiolar meristele probably had more than one strand of protoxylem. In the least ancient of the three families, the Osmundaceae, further removed from both the Zygopterideae and the common ancestor of the three families than the Botryopterideae, these characters seem to have been lost, though the diarch traces occasionally found near the stele in *Thamnopteris Schlechtendalii,* one of the oldest known of the Osmundaceae, may

be the last relics of a petiolar strand that originated phylogenetically as a branch. It is noticeable that most of the early Osmundaceae known to us are large forms, often attaining to the habit of small tree-ferns. In such, the appendicular nature of the leaf at its insertion on the stem might well be emphasized owing to coenogenetic enlargement of the latter.

The somewhat heterodox theory of the course of evolution of the petiolar bundle of the fern frond, advocated above, is in agreement with the now very generally accepted view that the frond was originally a dichotomous branch system; but it is in contradiction with the equally widely held view that in the Coenopterideae, if we trace the petiolar bundle back to its origin from the cauline stele, we shall find it assuming on the whole a more and more primitive form. It seems that a choice must be made between these two views, for it appears illogical to combine them. The view here advocated seems to be historically, *i.e.*, geologically, the stronger. It is not denied that the leaf-trace of the recent Osmundaceae and of the great bulk of the existing Leptosporangiatae is referable to a ground type represented by the C-shaped, monodesmic leaf-trace characteristic of the older Osmundaceae. Some details of this complicated evolution may be open to question; we may even find some forms retaining ancestral features not found in the typical C-shaped trace. But the general outline of the evolution of the leaf-trace and petiolar bundle in the Leptosporangiatae is clear from the work, to mention only a few writers, of Gwynne-Vaughan, C. E. Bertrand and Cornaille, and Professor Bower whose latest book gives a most helpful summary of these multifarious lines of evolution (*9, 345*). The issue at stake is the relation of this monodesmic C-shaped strand to yet earlier forms of vascular supply.

THE MICROPHYLLOUS OR MEGAPHYLLOUS NATURE OF THE REMAINING PHYLA

We have now briefly considered the forerunners of leafy vascular plants, the more primitive of the microphyllous types,[3] the forms leading to megaphyllous types and the early typically megaphyllous plants. There remains the question of which of the other phyla were microphyllous and which megaphyllous.

[3] Since the account of the "Yeringian fossil" was written (*11a*), Drs. Land and Cookson have published a fuller account of this plant and have named it *Baragwanathia longifolia*. Their studies are founded on further specimens, some of them of undoubted Mid-Silurian Age.

In the small phylum of the Cladoxylales, if its morphology may be interpreted in accordance with the structure of the Devonian *Cladoxylon scoparium* Kräusel & Weyland, we would seem to have a group of megaphyllous build, possessing also microphyllous leaflets that may be either repeatedly branched emergences or, more probably, small thalloid branchlets that have become laminar. But, as Dr. Sahni points out (42, *466, foot-note*), the reference of *C. scoparium* to the genus *Cladoxylon* is doubtful. The stelar anatomy is closely similar to that of the previously described species of the genus but there is no evidence that these shared the morphological peculiarities of *C. scoparium.*

Many botanists have regarded the Articulatales as microphyllous (1, 9, 21, 23, 52). Goebel, who in the last edition of his "Organographie der Pflanzen" considered only the recent members of the Articulatales, says that in the Equisetaceae the leaves have become smaller and more numerous during phylogeny (14, *1165*). This author regarded the large and small leaves of vascular plants as having a similar origin; for him, the size of the primitive leaves of a phylum was not necessarily a decisive factor in the classification of the phyla. Lignier (36), Scott (47) and Dr. Campbell (12), however, look upon the leaf of the Articulatales as primitively branched and more or less of the fern-type. Dr. Campbell's views are in striking contrast to those of other botanists. He thinks it probable that in the ancestors of recent ferns the vascular sporophyte was built up essentially of a large single leaf and of a protocorm or foot. He suggests that it is possible that from ancestral forms resembling the Anthocerotes two series of ferns were developed, one passing through intermediate forms resembling the Psilophytales and "resulting in a broad dichotomously divided frond with terminal sporangia, like *Cladoxylon,* and the other more directly developing the spike-like sporangiophore of *Ophioglossum* (12). He thinks that *Cladoxylon* and *Hyenia* may resemble the predecessors of modern ferns (presumably of his first series) and suggests that the fan-shaped body (aerial shoot) of *Hyenia* may correspond to the frond of the ferns. He accepts the affinity of *Calamophyton* with *Hyenia* and thinks it quite conceivable that from the latter's type of shoot there arose a typically megaphyllous and primarily monophyllous[4] series; while

[4] Numerous aerial shoots have been shown to be borne on the rhizome of *Hyenia elegans* Kr. & Weyl. (31).

in another direction another series led, through types such as *Hyenia* and *Calamophyton,* to *Asterocalamites* "where the relatively large leaves retain the primitive dichotomous branching" (12, *496*). These theories seem to be negatived by the very poor geological record of the Anthocerotes and Ophioglossaceae; by certain algal characters of the sporangia of the Rhyniaceae; by the fact that the developmental evidence points to the conclusions: (1) that the ophioglossaceous spike is of pinna nature; (2) that the species of *Botrychium,* with their more freely branched fronds, seem to be more primitive than *Ophioglossum,* the simpler leaved forms of the latter genus being apparently phylogenetically the more modified (*7, 87*); and by the existence in the Devonian and Carboniferous strata of numerous branch-like fronds and frond-like branch-systems intermediate between the *Psilophyton*-like spiny branch-systems and such fern-like fronds as those of some later Coenopteridaceae, *i.e.,* of species of *Etapteris* and *Anachoropteris.*

The Articulatales, however, do seem to be primitively megaphyllous. Their leaves may well have arisen from ramified thalloid axes which, though themselves dichotomous, were already lateral branches, borne sympodially on a relatively main trunk. An analogy may be found in the lateral fertile dichotomous branches of *Pseudosporochnus* (32). They may, therefore, have been smaller than some of the branch-systems that were converted into fern fronds. Moreover, verticillation, when it was acquired, would tend to reduce the size of the leaves, though in some dendroid Psaroniae the fronds were very large. Professor Bower accepts the simple but relatively wide and pluri-nerved leaves of some forms of *Sphenophyllum* as having arisen by webbing from the geologically older *Spenophyllum* leaves that were divided into narrow segments, but he holds that dichotomy is the simplest accommodation of form to increasing size and that it occurred also in the microphylls of the Articulatae (*9, 149, 160*). This is certainly true; apart from *Protolepidodendron Scharyanum* and *P. wahnbachense,* we know of various fossils possessing branched aphlebioid structures that almost certainly originated in evolution as emergences. Professor Bower also argues that the lateral origin of the leaf sheath—itself a highly modified structure—in the embryo supports the microphylly of the group (*9, 196*); but, as he himself points out, the details of an encapsulated embryo are subject to

plastic differences even within the limits of a single genus (9, *557*). The presence of relatively large and forking leaves in a number of the older Articulatales is a stronger argument. Let us consider the four main groups usually included under the Articulatales. In the oldest group, the Mid-Devonian Protoarticulatae, the leaves were once or repeatedly forked and in *Hyenia* attained a length of 2½ cm. In the Upper Devonian *Pseudobornia,* the only known genus of the Pseudoborniales, the leaves are much larger and so much cut and lobed that when first found, being detached, they were thought to be fern fronds (46, *110*). This genus, unfortunately not mentioned by Professor Bower in his latest book (9), presents a very great, one might almost say an insuperable, difficulty to accepting the Articulatales as primitively microphyllous. Dr. Zimmermann, who regards the Articulatales as primitively microphyllous, explains its large leaves by supposing that they originated by a confluence of ultimate ramifications, *i.e.,* by a process essentially similar to that by which he supposes fern-fronds to have arisen. The oldest undoubted members of the two remaining groups of the Articulatales, the Sphenophyllales and Equisetales, seem to be, respectively, the Upper Devonian *Sphenophyllum subtenerrimum* Nathorst and *Asterocalamites scrobiculatus* Schloth., which seem not to be certainly known below the Carboniferous (50, *266*). Both have repeatedly dichotomous leaves. From a study of the fertile shoots it would seem, as Professor Seward long ago noted, that the common stock from which Equisetales and Sphenophyllales arose must lie very far back (49, *388;* 10, *315*). Nevertheless, it is commonly accepted that they and the Pseudoborniales should be associated with the older Protoarticulatae in the same main phylum of vascular cryptogams and the fact that in all of these groups we find branched leaves borne on stems with continuous ribs seems to show a primitive ground plan of forked leaves for the whole phylum.[5] The Lower Devonian *Climaciophyton,* which has been held to be the oldest member of the Articulatales and has been

[5] Drs. Kräusel and Weyland (29, *326*) are mistaken in supposing that in a paper published in 1927 (10) the present writer laid great weight on one of their drawings of *Hyenia* as tending to show that the bundles in the Protoarticulatae had the course characteristic of calamitean bundles, *i.e.,* they alternated at the nodes. No such statement was made by the writer in that or in any other paper, though the drawing of theirs in question (28, *134* Fig. 16a) certainly suggests alternation of the bundles, which apparently does not occur.

provisionally compared to the Sphenophyllales (30), might be used in support of the primitive microphylly of the phylum. The small plants, but a few millimeters long, had irregular axes bearing whorls of three small and relatively thick, simple, sessile leaves. In the absence of fructifications and articulations, it is impossible to say to what phylum *Climaciophyton* belonged. Verticillation of the leaves occurs in the Lycopodiales, *e.g.,* in species of *Lycopodium* and of *Lepidodendron.* In *Drepanophycus spinosus* Krejci sp., a species of the Psilophytales, Drs. Kräusel and Weyland found that the small spine-like leaves were sometimes whorled (as in the examples described by Potonié as *Psilophyton bohemicum*) and sometimes spirally inserted (as in Potonié's *Psilophyton spinosum*) (32). Verticillation of the leaves is, therefore, by itself, no proof that *Climaciophyton* was a member of the Articulatales. It might equally well be a member of the Lycopodiales.

As regards the Noeggerathiales, though little is known of them, we may feel reasonably certain that their leaves were not emergences, though whether they, perhaps including *Barrandeina* and *Duisbergia,* represent an independent pseudomacrophyllous branch or are allied to the Articulatales, more particularly to the Sphenophyllales, is uncertain (11).

Most botanists look upon the Psilotales as primitively microphyllous. Some (*26, 839;* 40, *159; 9, 145*) think that they are probably nearer to the Psilophytales than to any other group, and their complete rootlessness, dichotomous branching and simple vegetative leaves, even if these be held to be somewhat reduced in *Psilotum,* certainly support this view. Scott, towards the end of his life, was inclined to look upon them as aberrant lycopods, which would also make them microphyllous (41, *397*). It is, however, possible, especially if the fertile appendages of *Psilotum* and *Tmesipteris* are regarded as forked sporophylls bearing a ventrally situated sporangiophore, that there may be some affinity between Sphenophyllales, Noeggerathiales and Psilotales. In this case, the last-mentioned group would presumably be megaphyllous and their vegetative leaves reduced. The nature of the fertile appendages lies, however, outside the scope of the present essay.[6]

In the above sketch the object has been to fix our attention on certain main lines of evolution which we seem able to discern, at

[6] A short summary of this question is given in 11.

least in part and fitfully. In doing this it has sometimes been necessary to consider forms of doubtful nature or of which we know very little because, although it is undesirable to base theories with a wide phylogenetic bearing on uncertain foundations (*29*, *326*), it is still more undesirable not to attempt to take stock of the position or to do so without considering all the relevant facts. Thus, where anomalous ill-preserved or incompletely understood forms seem to affect a question, the least unsafe course is to consider their supposed structure, bearing in mind the doubtful nature of such evidence. On the other hand, where such types stand more or less alone, or do not seem to bear on the theories under discussion, they have not been considered. But, in conclusion, as some of these forms are of the greatest interest to all students of the Pteridophyta, readers are referred to accounts, by various authors, of *Schizopodium* (19), *Haspia* (29), *Boegendorfia* (17) and *Thallomia* (20).

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A FRANK LETTER FROM THE EDITORS TO THE READERS OF THE BOTANICAL REVIEW

Please read it all. We want to tell you something and we want your advice.

First, a word of thanks. We are sincerely grateful to our subscribers for their financial support; without them, the first volume of the Review would have been the last; because of them, the Review looks forward to a long life of usefulness. We are equally grateful to the distinguished botanists who have written for us. We are also appreciative of the help generously given us by our editorial board. Subscribers, authors and advisors have been equally essential. We thank you all.

Second, a bit of history. The idea of the Botanical Review grew out of an unfulfilled desire. We wanted to know more about botanical progress but had no time to keep up with the voluminous and widely scattered periodical literature. So we began our plans in November, 1933. At the Boston meeting of the Botanical Society we explained these plans to a score of botanists and found them all enthusiastic. We immediately enlisted the help of a board of editors and according to their advice sent out requests for manuscript. To our surprise and delight scarcely a botanist declined an invitation to write.

But it takes time to write good botanical manuscript, and for a while we were not certain that we could publish our first number in January. Eventually manuscript began to come in, and since those first anxious weeks we have never been without copy.

Our next worry was about subscribers. We felt that our ideas were basically sound and were confident that the Review would soon succeed. But how about the first year? Printing costs money and bills must be paid. We estimated that we might get 200 subscribers the first year

and were prepared to lose nearly a thousand dollars on the first volume.

Our advertising circulars finally arrived and five minutes after they were unpacked we had our first subscriber. We were up to our expected two hundred when the January number appeared. By the middle of March we crossed the five hundred mark and had to increase the size of our edition. By June we passed seven hundred and again had to call for more copies. At the writing of this letter we are at the eight hundred mark and the Review is completely self-supporting.

In the advertising circulars we promised twelve numbers to a volume, containing about 32 pages each, or a total of 384 pages. The first nine numbers alone had 381 pages, so the volume will amount to about 500 pages. You are getting, consequently, 25% more reading matter than you expected. We also indicated that we would print three articles in a number, each with about ten pages. Not one article has been that short. Botanists apparently can not do a subject justice in so few pages or else the topics suggested for treatment are too inclusive. However, a topic too narrow in its scope is not practical. Its usefulness is more restricted and it is isolated from other very closely related subjects. Probably future experience will be about like the past, and you may look forward to articles averaging twenty pages in length.

Several articles by botanists of continental Europe have been submitted in French and German and have been translated by us. Both of us are reasonably proficient in the two languages and we have not hesitated to ask for help from others. We believe we have succeeded in presenting the authors' reviews correctly.

Bibliographic citations have bothered us greatly. Verification of some references has been impossible in New York. In such cases we have had to follow the contributor's copy. Undoubtedly many errors have slipped in. We hope they have not been serious or misleading.

At present there is scarcely an American college or university where botany is taught which does not subscribe to the Botanical Review, some of them with several copies. The number of individual subscribers is impressive. A professor in one of our largest institutions, botanically speaking, tells us that the Review is the one magazine which every graduate student reads from cover to cover. We are proud of our success.

Third, a request for advice. We want the Review to please you and to be useful to you. We can not tell how you feel about it if you do not let us know personally. Won't you indicate, on the margin, your opinion about the following points and send it to us along with a renewal of your subscription.

1. What do you think of the length of the articles? Are they too long or too short?

2. Are the articles sufficiently diversified? Is any field of botany receiving too much or too little attention?

3. Is there any particular topic which you would like to have presented? Our advisory editors may think the time is not ripe for discussion of a particular subject or a satisfactory author may not be available. We will, however, give due thought to every suggestion.

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8. Is there any other feature of the magazine which you wish to criticize or which you believe could be improved or omitted?

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H. A. Gleason,
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INSECTS IN RELATION TO PLANT DISEASES[1]

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INTRODUCTION

Forty-three years ago Waite (78) reported his experiments with the honey-bee and fire-blight of pears, in which he demonstrated for the first time that insects could act as vectors for a plant disease. Today, after forty-three years of intensive research in plant pathology, the degree of importance of bees in the epiphytology of fire-blight is still a debatable question. Rosen (60), on the one hand, contends that the beehive is a source of primary infection and a factor of prime importance in the development of epiphytotics of fire-blight. On the other hand, Pierstoff and Lamb (50), Hildebrand (31) and Thomas and Ark (76) maintain that the pathogen does not survive in the hive and that the hive is of no significance in initiating fire-blight epiphytotics. In a similar way the evidence presented by Tullis (77) in 1929, minimizing the rôle of aphids in the spread of fire-blight as presented in the earlier work of Stewart and Leonard (72) and Merrill (45, 46), leaves this aspect of the problem also in an equally uncertain state. A review of all the work dealing with insects as a factor in the spread and development of fire-blight impresses one with the fragmentary, superficial and conflicting nature of much of the evidence presented.

This situation is cited primarily as an example of the unsatisfactory nature of much of our information on the rôle of insects in the spread and development of plant diseases. It is the writer's opinion that this field of research has not received the attention that its nature and importance justify. This would seem to be an opportune time to review the subject in such a way that its importance and promise as a field of research may be made evident.

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[2] For several years the writer and Dr. A. A. Granovsky, of the Division of Entomology, have been associated in teaching a course on the relation of insects to plant diseases. The writer wishes to express his appreciation to Dr. Granovsky for critically reading the manuscript.

THE VARIED RELATIONSHIPS OF INSECTS AND PLANT DISEASES

In the minds of many people the association of insects with plant diseases is limited to the simple process of dissemination. Although other aspects have been recognized, the idea of dissemination has almost exclusively predominated in all published literature of a general nature on the subject (6, 54, 55).

To disseminate is to scatter, broadcast or diffuse. To inoculate, as the term is used in plant pathology, is to transport inoculum to a particular part of the plant where infection may result. Wind is a common agent of dissemination but inoculation occurs only when by chance the inoculum falls in the right place. Many insects, because of their habits of visiting certain species of plants and specific organs of those plants, are not only agents of dissemination but also very effective agents of inoculation. The honey-bee and blossom-blight of fruits (78), the sphinx-moth and anther-smut of pinks (8) and pollen-eating flies and ergot of cereals (1) are well known examples of this type of insect inoculation. More recently described associations of this type are those involved in the so-called fruit spoilage of figs (69). Endosepsis (12), souring (13) and smut (49) all depend upon certain fig insects for introducing the respective inocula into the interior of the young fig fruit.

The systemic disease of red clover caused by *Botrytis anthophila* Bond., recently described by Silow (64), is especially illustrative. The spores of this pathogen are transported by the bees that pollinate red clover. The spores along with pollen grains are deposited on the stigma where they germinate. The mycelium of the pathogen grows into the developing seed and persists under the seed coat. When such infected seeds are planted they give rise to systemically infected plants. The fungus grows out into the young flowers, many of which are blighted, and the spores are formed over the surface of the anthers. Bees visiting such blighted blossoms become contaminated with spores and spread the infection to other plants.

All of our higher plants have an effective natural protection against pathogens in the form of cuticle or cork. The entrance or penetration through this external covering by the pathogen has been termed "ingress" by Whetzel (79). Some pathogens are able

to penetrate this protective layer by their own resources but many depend upon wounds. The feeding or oviposition wounds of insects constitute one of the most important avenues of ingress for plant pathogens. The significance of insects as agents of dissemination and inoculation is greatly enhanced when they serve also as agents of ingress. In some cases this aid to ingress overshadows the importance of dissemination and inoculation. The rôle of the woolly aphid in the development of perennial canker of apple trees as described by Childs (19) and McLarty (44) is an excellent example of this type of relationship. These investigators have shown that *Gleosporium perennans* Zeller is strictly a wound parasite and that reinfection of a canker must take place each year. Although plenty of inoculum is present in the canker, reinfection does not occur in the absence of the aphid. The aphids live in the crevices of the canker and make the wounds which are necessary for infection on each suceeding year's growth of callus. Thus the so-called "perennial" canker is actually annual and the apparently perennial character depends entirely on reinfection each year through wounds made by the aphids.

Banfield (3) and Riker and Hildebrand (59) have recently shown that white grubs and several other soil insects play an important part in the opening of infection courts for crown gall, although they are probably of little significance in dissemination of the pathogen.

The vulnerable point in the life history of many pathogens is in their inability to survive the winter period or other adverse conditions of the environment. In recent years many pathogens have been shown to hibernate in the body of insects where they are adequately protected against changes in humidity and temperature, against competition with other organisms and against other adverse conditions. Furthermore, pathogens which hibernate in the body of such insect vectors are in the most strategic position for prompt and successful primary infection in the spring. Rand and Enlows (53, 54) have shown that *Bacillus tracheiphilus* E. F. S., causing cucurbit wilt, survives the winter in the bodies of hibernating adults of the striped cucumber beetle and that this is probably its only method of survival. The recent proof by Poos and Elliot (52) that *Aplanobacter stewarti* (E. F. S.) McCulloch overwinters within the bodies of hibernating adults of the flea beetle, *Chae-*

tocnema pulicaria Melsheimer, has thrown much light on the epiphytology of the wilt disease of sweet corn. Similar survival in overwintering adult insects has been demonstrated for the blue-stain fungi, *Ceratostomella ips* Rumbold and *Tubercularilla ips* L., O. and C. and the pine bark beetles *Ips pini* Say and *Ips grandicollis* Eichh. by Leach, Orr and Christensen (40). The pathogen of the Dutch Elm disease, *Ceratostomella ulmi* (Schwarz) Buisman, apparently survives in a similar manner in the bodies of *Scolytus multistriatus* Marsh and *S. scolytus* Fab. (4, 27, 28, 43). It is also of considerable significance that plant pathogens may survive within the puparium of certain insects during the process of metamorphosis and be present in considerable numbers in the intestinal tract of the newly emerged adult. This has been demonstrated by Petri (48) working with the olive fly, *Dacus oleae* Rossi, and the olive knot pathogen, *Bacillus savastonoi* E. F. S., and by Leach (38, 39) working with the seed-corn maggot, *Hylemyia cilicrura* Rond. and *Bacillus carotovorus* Jones. In the case of the olive fly the bacteria are also transmitted internally through the eggs but the eggs of the seed-corn maggot, although often surface contaminated at oviposition, are always internally sterile.

INSECTS AND VIRUS DISEASES

In recent years striking progress has been made in the study of the virus diseases of plants (68). A formidable list of diseases and their insect vectors has been built up. An analysis of the accumulated data shows that there must be extremely varied and complicated biological relations between some of the viruses and their insect vectors. Up to the present time, however, relatively little exact information is available about the more intimate biological relations between insects and viruses (67). The surface has been merely scratched and it would be decidededly rash to attempt to generalize extensively on the data available. Nevertheless, some recent work is indicative of results that may be obtained when a concerted effort is made on this fascinating but perplexing problem. Only a few of the more significant facts will be mentioned here.

Many virus diseases are highly infectious and are easily transmitted by mechanical means. Others apparently can not be mechanically transmitted but are readily transmitted by certain rather

specific insect vectors. At the present time about 25 reasonably well studied diseases fall in the latter group. These are said to be biologically transmitted and an incubation period of varying length within the body of the insect vector is required in all cases. These "biological" insect vectors include about 15 leaf hoppers, 10 or 12 aphids, 2 species of thrips and 1 white fly. It is the nature of this biological association between virus and insect vector that especially needs elucidation.

Interesting and suggestive is the recent work of Storey (74, 75) who showed that in *Cicadulina mbila* Naude, the vector of maize streak, the ability to transmit the virus is inherited as a simple dominant sex-linked Mendelian factor. Those individuals inheriting the ability to transmit the virus were termed "active." Individuals not inheriting the ability to transmit the disease ("inactive") did not become viruliferous by feeding on infected plants but were made infective by directly inoculating the insect with the virus by means of a micropipette. Evidence was presented to show that in "active" insects the virus entered the intestines by the mouth and passed through the intestinal wall into the blood, but that in "inactive" insects the virus could not pass through the intestinal wall. When the virus was injected into the blood with a micropipette, the insect became viruliferous and was able to transmit the virus to plants. Transmission was somewhat more irregular than with normal "active" insects and such artificially activated vectors usually became non-infective after varying periods of time, while normal "active" insects remained infective until death.

When "active" insects were fed on infected plants the virus could be demonstrated in the blood after 6 to 9 hours, while the insect could not transmit the virus to plants before 12 to 15 hours after feeding on infected plants. This is added evidence that the blood is the vehicle by which the virus is transported to the salivary glands.

Of equal interest is the recent report by Fukushi (29) that a virus causing a mosaic of rice and transmitted by the leaf hopper *Nephotettix apicolis* Motsch is transmitted from generation to generation of the insect vector through the egg. If this work is verified, it will be the first definitely proven case of the transmission of a plant virus through the egg of its insect vector.

The biological association of viruses with thrips presents another significant variation. Samuel and Bald (61) working with *Frankliniella insularis* Frankl. and spotted wilt of tomato and Linford (41, 42) working with *Thrips tabaci* Lind. and pineapple yellow-spot showed that adults do not become viruliferous when fed on diseased plants but that young larvae become infective after a period of ten days and that they remain viruliferous through pupation. Thus adults are infectious only when reared from viruliferous larvae.

The nature of the relationship between virus and insect vectors offers considerable promise as a criterion for virus classification. Elze (22), Storey (73) and Johnson and Hoggan (34) have all published schemes of classification in which such relationships play a prominent part. Kunkel (37) considers insect relationships as one of the most useful criteria for differentiation and classification of viruses. A better understanding of the nature of the biological relationships between viruses and their insect vectors obviously will be an important step in the solution of the virus problem.

INSECTS AND NON-PARASITIC DISEASES

When considering insects in their relation to plant diseases one must not overlook those non-infectious diseases that follow insect feeding but are not caused by any known microorganism or virus. One of the best known diseases of this type is the so-called hopper burn of potatoes or yellow top of alfalfa shown by Ball (2) and Jones and Granovsky (35) to be caused by the feeding of the potato leaf hopper *Empoasca fabae* Harris.

The earlier work of Granovsky (30), Monteith and Hollowell (47), Poos (51) and others (23, 26) led to the suggestion that the probable cause was a diffusable toxic substance or enzyme injected into the plant by the leaf hopper. In 1930 Granovsky (30) reported that microchemical tests revealed a greater accumulation of starch grains and sugars in affected tissues. There was also a clogging of vascular bundles and complete disorganization of the phloem region of severely injured tissue, phenomena held to be due to enzymic secretions by leaf hoppers in the course of feeding. Later investigations by Smith and Poos (66), Smith (65) and Johnson (33) have verified the histological changes reported by Granovsky (30) but these authors consider it improbable that the

leaf hopper injects a toxic substance. They suggest that the over-accumulation of carbohydrate products of photosynthesis above the points of feeding are sufficient to cause the symptoms usually attributed to a diffusable toxic substance.

In contrast to hopper burn of potatoes is the psyllid yellows described by Richards (57) and Richards and Blood (58). This striking disease is caused by the feeding of a considerable number of the psyllid, *Paratrioza cockerelli* Sulc. The disease is systemic and causes profound abnormalities in the physiology of the plant. In addition to other striking symptoms, tuberization is inhibited, often to a degree sufficient to cause a total loss of the crop. There is little direct evidence as to the nature of the injury. Although Binkley (5) has designated the trouble as a virus disease and Shapovalov (63) has reported tuber transmission, their results do not agree with the more extensive work of Richards and Blood (58). The results obtained by the latter workers point to the presence of some toxic substance introduced by the insects while feeding.

The mealy-bug wilt and green-spotting diseases of pineapples, originally described by Illingworth (32) and studied further by Carter (15, 16), are perhaps the most interesting diseases of this type. According to Carter (15) mealy-bug wilt is caused by a phytotoxic secretion of the mealy-bug *Pseudococcus brevipes* Ckl. Plants are wilted suddenly only when the initial population of mealy-bugs is relatively large. When the initial population is small the plant builds up an antitoxic reaction and does not wilt until the population is excessively large. The toxicity of the insects is influenced by the host plants previously fed upon.

The green-spotting disease is caused by the same insect but is distinct from wilt (16). It also is caused by a phytotoxic secretion of the insect. The toxic principle in this case is correlated with the presence of certain symbiotic rod-shaped bacteria in the mycetome of the mealy-bug. The symbiotic bacteria are not present in all insects but when present may be transmitted from mother to young. The presence of the symbiotic bacteria and the toxicity of the insect depend on the plants upon which the insect has fed. After the insects have fed for two generations on *Panicum barbinode* the bacteria are lost and the insects become non-toxic (17, 18).

The almost universal presence of mycetomes and their intracellular symbiont in Homopterous plant-sucking insects as reported by Buchner (10) and others makes this work very significant and justifies further studies of these symbionts in relation to insects associated with plant disease both infectious and non-infectious.

THE BIOLOGIC AND EVOLUTIONARY SIGNIFICANCE OF THE ASSOCIATION OF INSECTS AND PLANT PATHOGENS

Research workers in phytopathology have, as a rule, considered insects merely as one of several agencies of inoculum dissemination to be disposed of in the ordinary routine study of a disease. It is the opinion of the writer that the relation of insects to plant diseases is too important and too complex to be handled in such a summary manner. The association of insects with plant pathogens is, for the most part, not a mere haphazard matter of chance but rather a highly organized relationship which, in many cases, may have arisen out of a close association of insects and microorganisms over a period of 50 million years or more. It is a definite biologic phenomenon of evolutionary significance and has broad biologic and economic implications. As such it deserves more than routine attention. It deserves the same type of sustained and coordinated thought and effort that has been given to other phytopathological problems of fundamental nature.

As a biologic phenomenon the association of insects and plant pathogens is in many respects similar to that of entomophily, i.e., insect pollination. All students of botany or of entomology are familiar with the remarkable evolutionary adaptations of insects and flowers. It will not be necessary here to describe the various details of these adaptations. Along with the morphological adaptations on the part of both insects and flowers there has been built up a constant and regular association of insects and plants that is mutually beneficial to both parties of the association. Let us consider how this association came about. It is agreed by most, if not all, students of plants that our most primitive flowering land plants were wind pollinated. The pollen grains were disseminated by the wind and pollination was accomplished only when, by chance, a pollen grain accidentally fell upon a stigma of the proper species. This necessitated the production of enormous quantities of pollen and resulted in a tremendous waste of materials. That this was

true is abundantly verified by the geological records of the plants of the Carboniferous age. But in one fortunate period long ago, insects discovered the food value of pollen and perhaps the associated secretion of nectar and began to make regular visits to the source of supply. In this way the pollen was transported with very little loss to the stigmatic surface of the proper plant. This association had a survival value for both insects and flowering plant and consequently has persisted throughout the ages and has developed to a state of very high efficiency. A little reflection will show that the principle underlying this association is essentially the same as that underlying that of insect dissemination of plant pathogens. Some pathogens are disseminated only by wind. In such cases relatively large quantities of inoculum are produced but only small amounts reach an infection court and survive. Other pathogens have become associated with insects which transport them or their spores to the required infection court with a minimum of waste and a maximum of efficiency, especially when the insects provide also a means of ingress and of protection against the elements. This type of association, like insect pollination, also has a survival value and numerous cases have persisted with remarkable adaptations on the part of both insect and pathogen. Although survival value does not predicate benefits by both insect and pathogen, there are numerous cases of striking mutual benefit and interdependence.

But it would not be fair to drop the comparison here for there are other important factors which have influenced the complicated adaptations associated with entomophily. With the development of insect pollination the nature of the process led to an increase in cross-pollination in comparison with self-pollination. Cross-pollination increased the frequency of hybridization and this in turn stimulated variation, a primary factor in evolution. Thus insect pollination by stimulating hybridization and variation has speeded up the development of entomophily itself. This factor, so important in evolution, is apparently lacking in many of the associations of insects and plant pathogens and may account for the fact that the latter association is less obvious than entomophily.

But recent investigations have shown us that the factor can not be entirely removed from the picture. With the discovery of heterothallism in fungi by Blakeslee (7) and its further elucidation

by Kniep (36), Buller (11), Stakman *et al.* (71) and others the signification of hybridization in the evolution of fungi is more clearly discernible.

Brodie (9) has shown how flies are agents of "diploidization" in the fungus *Coprinus lagopus,* a process fundamentally analogous to insect pollination of higher plants. *Coprinus lagopus* is a heterothallic fungus. Each basidiospore formed on the "inky-cap" mushroom, upon germination, forms a homosexual mycelium which is unable to reproduce the mushroom stage until it has been fertilized or diploidized by fusion with a mycelium of the opposite or complementary sex. Each of these mycelia produces spores in drops of a sticky solution which is attractive to flies. Flies, by feeding on these droplets, transport spores from one mycelium to another. The spores promptly germinate and fuse with mycelia of opposite sex resulting in diploidization and the formation of the mushroom stage. Dowding (21) also has pointed out a similar association between *Ascobolus stercorarius* (Bull.) Schröt. and mites and flies.

A similar case has been revealed by the work of Craige (20) on *Puccinia graminis,* the well known wheat-rust pathogen. In this heterothallic fungus diploidization occurs on the barberry leaf. Flies, attracted by the drops of sugary solution formed on the bright orange colored pycnia, often transport the pycnospores from one pycnium to the other. Thus insect transportation of pycnospores increases the chances of hybridization. The large number of physiologic forms which occur in this pathogen can be explained to a large extent by the hybridization that occurs on the barberry (71). Is it merely a coincidence that such specialized adaptation for insect "pollination" of a fungus, with resulting hybridization, should be found in one of the most highly developed plant pathogens and one in which physiological specialization has reached such a high state of development?

SYMBIOSIS BETWEEN INSECTS AND MICROORGANISMS AND ITS SIGNIFICANCE IN PLANT PATHOLOGY

In the preceding discussion we have been concerned primarily with the association of insects and those fungi and bacteria which are plant pathogens. But the association with insects is by no means confined to pathogenic microorganisms. In all probability

the association arose first among the non-pathogenic forms. The work of Paul Buchner (10) and his students, summarized in his book "Tier und Pflanze in Symbiose" published in 1930, has shown us the astounding universality of symbiosis between insects and microorganisms and the high degree of development it has reached. Buchner's investigations are of great significance to the student of insects in their relation to plant diseases. They have shown that symbiosis with microorganisms is to be found in nearly all orders of insects and that in some groups such as those feeding on plant sap and on wood it is almost universal. In several cases the symbiotic microorganisms have proven pathogenic to plants. His studies of the subject have yielded sufficient evidence to justify the conclusion that the interrelations of insects and symbiotic microorganisms are as complex as, and of evolutionary significance equal to, those between insects and flowering plants. The almost universal occurrence of symbiosis between insects and microorganisms in general, coupled with the numerous striking cases involving plant pathogens, in the writer's opinion, makes it imperative that we recognize its importance and significance in the study of plant diseases.

THE POSSIBLE RÔLE OF INSECTS IN THE ORIGIN OF NEW DISEASES AND THE EXTENSION OF OLD ONES

There is one other aspect of the association of insects and plant diseases that is generally overlooked. This is the possible and probable rôle of insects in the sudden appearance of new and destructive plant diseases. We are accustomed to thinking of plant diseases largely in terms of the pathogen, an organism of ancient lineage which, in common with other plants, has had a long and slow process of evolution during which its efficiency as a pathogen has also evolved. But a disease is not an organism. It is a biological process. It is the result of the interaction of two or more organisms, influenced by a host of other factors. When it is considered in this light we are faced with the possibility that many of our plant diseases may be of relatively recent origin. For the purpose of illustration let us consider the Dutch Elm disease. This disease was first recognized in South Holland in 1919 (62, 70). There seems to be considerable evidence that it has spread from this center to most of the countries of southern and western Europe

and it has been introduced also into the United States (43). Its origin is obscure but the general assumption seems to be that it may have been introduced into western Europe from some other part of the world. The writer does not wish to challenge this assumption, for he has no evidence to offer, but it is suggested that as a disease in the sense of a biological process it may be entirely possible that it had its origin in western Europe within relatively recent years. The bark beetles that constitute the principal agent of dissemination of *Ceratostomella ulmi* were known in Europe and America for many years prior to the appearance of the Dutch Elm disease (25). At the present time there are large areas in which the beetles occur but where the disease is absent (25), but these areas appear to be rapidly diminishing. This fact, although by no means conclusive, would seem to indicate that the association is probably not one of long standing. *Ceratostomella ulmi,* although a virulent pathogen on elms, grows well as a saprophyte on dead wood or bark. It apparently is not well adapted to wind dissemination and apparently can infect only through wounds. In the absence of a suitable insect vector it would probably exist chiefly as a saprophyte on dead wood and perhaps be disseminated from one dead tree to another by insects inhabiting dead wood. As such it would attract no attention and would scarcely justify consideration as a disease. But when it becomes associated with the Scolytus bark beetles, which prove to be ideal vectors, there suddenly appears a very destructive disease. Not only this, but the elm bark beetles, which by their nature can breed only in weakened or dying elm trees, find the association to their advantage. By transporting the spores of *Ceratostomella ulmi* and introducing them into feeding wounds they provide themselves with an abundance of dead and dying elms and thereby rapidly increase in number. More vectors, more disease, more dead trees, and more vectors! A vicious circle that results in an epiphytotic disease that threatens to destroy one of our most valuable trees. This order of events in the origin of the Dutch Elm disease is purely theoretical but it is well within the realm of possibility and deserves consideration. It is suggested here primarily to illustrate one of the many significant aspects of the association of insects with plant diseases. Many insects as well as plant pathogens are, or until recently have been, relatively local in their distribution. With in-

creased commerce and travel throughout the world they are becoming more widespread in spite of all of our efforts to control them. With promiscuous intermingling of insects and pathogens would it not be surprising if new combinations and associations were not formed in which an insect and a pathogen (neither of which alone may be conspicuous or of economic importance) working together may give rise to a destructive disease?

The invasion of new areas by insects may also profoundly influence the distribution of certain well known destructive diseases. Curly top of sugar beet, for example, is limited in its distribution in North America to the arid regions of western United States. According to Carter (14) this is true because the insect vector (*Eutettix tenellus*) can not thrive in the more humid regions. It recently has been shown by Fawcett (24) that curly top in Argentina is spread by another leaf hopper, *Agallia stictocollis*. This insect is said to thrive in regions of relatively high humidity. If it should be introduced into the United States, it is very probable that the range of curly top would be greatly extended.

THE FUTURE DEVELOPMENT OF RESEARCH IN THE FIELD OF INSECTS IN RELATION TO PLANT DISEASES

In 1920 Rand and Pierce (55) published an article entitled "A coördination of our knowledge of insect transmission in plant and animal diseases." This was the first general discussion of insects in relation to plant diseases to be published. As a result of the interest created by this article the American Phytopathological Society and the American Association of Economic Entomologists at their annual meetings in Toronto, Canada, on December 31, 1921, held a joint symposium on "Insects as disseminators of plant diseases" (56). One of the results of this symposium was to make more evident the need for closer coöperation between entomologist and plant pathologist. In spite of this evident need the situation today leaves much to be desired.

The lack of adequate coöperation is frequently but not always due to the human and personal element. The causes may be administrative or political; and still others may be matters of tradition. It is the writer's opinion that the wide gap separating research in the two fields of plant pathology and entomology is mainly traditional in nature.

Although entomology and phytopathology have one large problem in common, the protection of plants, the two fields of science have widely divergent outlooks. Not so many years ago there was a single branch of science known as biology and it was possible for one man to obtain a fair knowledge of the entire field. But this is not true today. Early in its history biology became sharply divided into the two fields of botany and zoology. Each of these fields has been divided and subdivided almost *ad infinitum*. Today two young students of biology start out together but very soon they come to the parting of the ways, one to become a zoologist, the other a botanist. After many years of training one becomes an entomologist, the other a plant pathologist, and they meet again both faced with the problem of plant protection. They realize the necessity of coöperative effort and make an attempt to coöperate, but lo! and behold! "They don't talk the same language." Their training has been too widely separated and too specialized. This condition of affairs has resulted in the neglect of a large field of information that is vital to the problem of plant protection.

The writer does not think that this difficulty can be avoided by the expedient of coöperation alone. Before these two workers can coöperate effectively they must be able to understand and speak a common language. Coöperative work is sometimes attempted on the principle of strict division of labor in which all "entomological" work is done by the entomologist and all "plant pathological" work by the plant pathologist. This type of coöperation is doomed to failure. In the problem of insects in their relation to plant diseases no such division is possible. For the greatest success the invisible, though very real, wall separating the two fields of research must be broken down. This may be rather difficult but it can be done. A first step in this direction would be a modification of our educational procedure so that research workers would be given the training and viewpoint necessary for the solution of the problem in hand. The worker must have a thorough knowledge of the essentials of both entomological and microbiological technic. He must have in his own mental make-up the viewpoint of both entomologist and plant pathologist. When these qualifications are combined in one man many of the difficulties of coöperation will be avoided.

A second step would be a liberalization of the narrow professional viewpoint which in effect often hangs out a sign reading: "This is the phytopathological field; all entomologists keep off," or "This is the entomological field; phytopathologists encroach at their own risk." Such a viewpoint may simplify some of the problems of organization but it is not conducive to the solution of these neglected borderline problems. The necessity of well defined fields of research, with corresponding responsibility and authority, is well recognized. Such responsibility and authority is necessary, not only for effective administration, but also for the existence of the guild spirit which is so important in scientific research. Nevertheless, when attempts are made to draw too sharp a line between related fields of activity many problems of vital importance and significance are usually neglected.

Even when coöperative relationships are cordial the sharp line separating the two traditional fields often results in a shifting of responsibility that is not conducive to efficiency. The plant pathologist with his vague knowledge of insects finds it easy, when faced with an insect-disease complex, to shirk his responsibility by saying, "That's up to the entomologist." Likewise the entomologist finds it equally easy to shy away from any problem that might involve a mycological or bacteriological study.

The importance of insects in relation to human diseases has led to the development of the rapidly growing field of medical entomology. It is manned by investigators trained in the fundamentals of both entomology and medical science. They have for their goal the solution of a particular kind of problem, namely, the rôle of insects in the spread and development of human and animal diseases. It would seem that the time is ripe for a similar development in the field of plant pathology.

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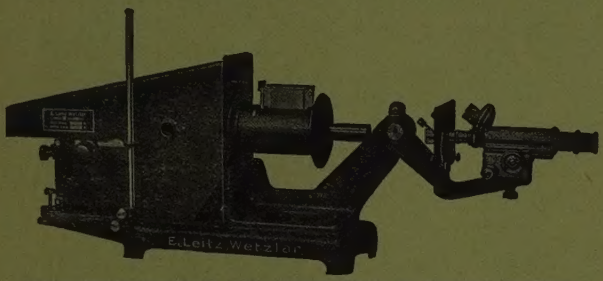

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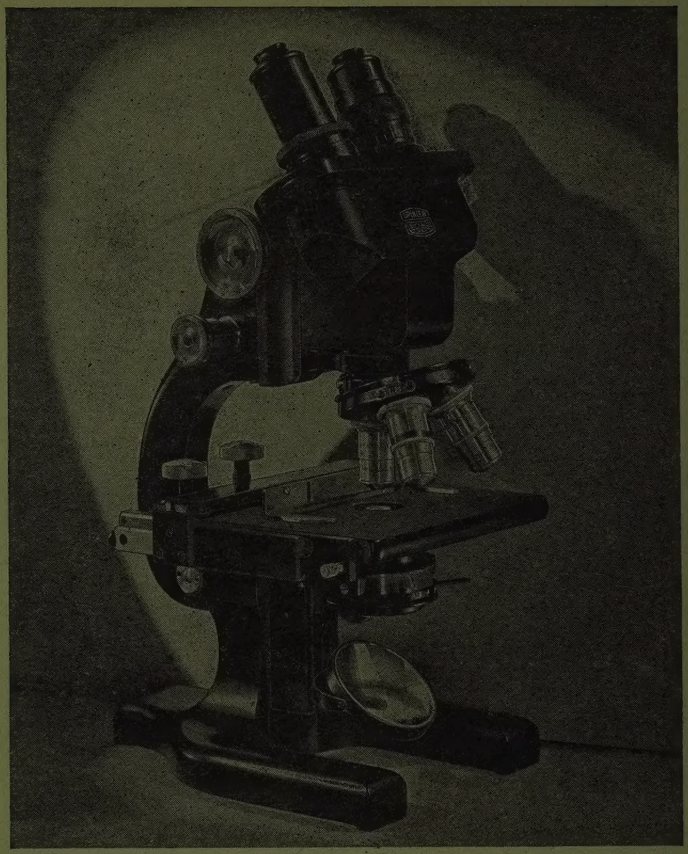

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